

# Not using the obvious: desert ants, *Melophorus bagoti*, learn local vectors but not beacons in an arena

Eric L. G. Legge · Marcia L. Spetch · Ken Cheng

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**Abstract** Many ant species travel large distances to find food, sometimes covering distances that are up to one million times their body length. Even when these foraging trips follow convoluted paths, the ants usually find their way back to their nest with precision (Wehner et al. in J Exp Biol 199:129–140, 1996). Ants have been shown to use both compass cues in the sky (pattern of polarised light) and landmarks on Earth to return to their nest. We present two experiments conducted on a solitary foraging ant: *Melophorus bagoti* in their natural habitat in the central Australian desert. Ants were trained and tested in situ. We tested foragers' ability to exit a circular arena which provided an undifferentiated panorama. Artificial visual landmarks were located near a small exit. On tests in which path integration information was not available, foragers did not use artificial landmarks as beacons. Instead, they oriented in the learned exit direction, whether or not it pointed to the nest. We suggest that *M. bagoti* foragers learned a context-specific local vector when cued by the context of the circular arena. Our findings present the first evidence that *M. bagoti* foragers learn context-specific compass directions to chart their initial path home.

**Keywords** Desert ant · Landmarks · Local vectors · *Melophorus bagoti* · Navigation · Orientation · Sky compass · Spatial localisation · Arena · Context

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E. L. G. Legge (✉) · M. L. Spetch  
Department of Psychology, BSP 217,  
University of Alberta, Edmonton, AB, T6G 2E9, Canada  
e-mail: elege@ualberta.ca

K. Cheng  
Department of Brain, Behaviour and Evolution,  
Macquarie University, Sydney, NSW, Australia

Many ant species travel large distances to find food, sometimes travelling distances up to one million times their body length (Wehner et al. 1996). Even when these trips are lengthy and follow convoluted paths, the ants usually find their way back to their nest with precision (Wehner et al. 1996). While the mechanisms by which ants navigate vary widely across genus and habitat, many ants have been shown to use visual cues to some degree (e.g. Franks et al. 2007; Graham and Collett 2002; McLeman et al. 2002; Vilela et al. 1987). For example, North African desert ants (*Cataglyphis fortis*) have been shown to rely heavily on compass cues that stem predominantly from the pattern of polarised light (Wehner and Müller 2006; Wehner 2003). Additionally, *Cataglyphis* ants have also been shown to use context-specific local vectors in certain situations (Cheng 2006; Collett et al. 1998). For example, Collett et al.'s (1998) *Cataglyphis* ants learned to head south when coming out of an experimentally provided channel, and this context-specific local vector appeared to be controlled by compass cues. Thus, in this case, it is thought that the unique visual panorama of the experimentally provided channel cued the ants to head south at the first available opportunity, upon exiting from the channel.

In addition to compass cues and local vectors, many ant species have also been shown to use landmarks for navigation. Landmarks are generally used as beacons, towards which the ants aim while travelling along a fixed route. These landmarks then function as an intermediate goal along their route, thus allowing them to break their route into more manageable segments (Graham et al. 2003; Nicholson et al. 1999). Furthermore, some ant species have also been shown to memorise arrays of landmarks surrounding their nest or reliable feeding sites (Graham et al. 2004; Narendra et al. 2007; Wehner and Räber 1979), thus

increasing their navigational precision and reducing the amount of time they spend searching for their goal.

One species that has been shown to use landmarks for navigation along a fixed route (Kohler and Wehner 2005; Narendra 2007b) and for locating their nest and reliable food sources (Narendra et al. 2007) is the Central Australian desert ant, *Melophous bagoti*, which resides in the feature rich, semi-arid deserts of Central Australia. When foraging, *M. bagoti*'s use of visual cues for defining routes and pinpointing target locations is similar to *Cataglyphis* ants (Cheng et al. 2009; Wehner and R ber 1979), wood ants (*Formica rufa*: Graham et al. 2003; Graham and Collett 2006; Harris et al. 2005;), and rain forest ants (*Gigantiops destructor*: Macquart et al. 2006; Wystrach and Beugnon 2009). Additionally, similar to wood ants (Fukushi 2001; Fukushi and Wehner 2004), *M. bagoti* has been shown to use panoramic visual cues (Graham and Cheng 2009a, b; Narendra 2007b). Specifically, Graham and Cheng (2009a, b) found that *M. bagoti* foragers used the contrast between terrestrial objects and skyline when navigating and that the lower 27° of elevation in the panorama was attended to the most.

Our research was designed to extend knowledge of the cues used by *M. bagoti* as they initially leave a feeding site to head back to the nest. We know that *M. bagoti* foragers sometimes follow fixed, idiosyncratic routes between a food source and their nest (Kohler and Wehner 2005) using both path integration (Narendra 2007a) and visual landmarks (Narendra 2007b). We also know that they use visual landmarks placed at the nest (Narendra et al. 2007), as well as visual panorama cues at the feeding site (Graham and Cheng 2009b). We do not know, however, whether they would use a specific landmark at a food source as a beacon to set the initial course home, and if so, how use of this cue might interact with other cues. We also do not know whether *M. bagoti*, like *Cataglyphis* ants, learn context-specific compass-based local vectors to return from a feeding site. Thus, our experiments provide the first test of whether *M. bagoti* will use beacons or a learned context-specific compass direction to start the journey home from a feeding site.

In order to address these questions, we provided ants with a feeder placed in the centre of a cue-controlled arena in their natural habitat. The arena allowed us to control the landmark information available to the ants and it provided only a single exit, which we marked with a visual landmark to serve as a beacon. The top of the arena was open, thereby allowing the ants to use compass cues to form a local vector. After ants had learned to enter and exit the arena readily, we then rotated the landmark to determine whether the landmark was used and how it interacted with other cues.

Our general strategy in these experiments was to train ants in situ to find food within our enclosed arena. Finding the feeder should not be a problem because numerous natural cues could be used on the outward route to find the

entrance to the arena. Once ants had obtained a piece of food from the feeder, they had to locate a small exit in the arena in order to return home. However, from inside the arena, natural terrestrial landmark cues were blocked from view by the arena walls. This allowed us to control and manipulate the cues available to the ants from within the arena that would help them locate the exit.

In our experiments, we provided ants with visual cues above or beside the exit, cues that we thought might serve as beacons. Additionally, we left the top of the arena open, which provided the ants with access to celestial compass cues. The ants therefore could learn to use the landmarks as beacons, and/or they could learn a context-specific local vector based on celestial compass cues. After training, we conducted tests to determine whether they used one or both of these cues. On tests, before transporting ants to a test arena, we allowed them to complete their homeward journey from the training arena and captured them when they started to search for their nest. Previous research has shown that *M. bagoti* no longer retain a homeward vector once they start searching for the nest (e.g. Graham and Cheng 2009a; Narendra 2007b). Thus, this procedure allowed us to nullify any effects of path integration on orientation in testing.

We conducted two experiments, using ants from separate nests. The first experiment provided a solitary landmark located above the exit of an artificial arena. In this experiment, the arena exit was aligned with the nest such that the compass direction to the exit was the same as the homeward compass direction. The second experiment used a set of three-dimensional landmarks on each side of the arena exit. Moreover, the exit was rotated away from the nest-feeder direction so that there was a large disparity between the compass direction to the exit and the homeward compass direction. Tests in which we rotated the landmark in an identical arena allowed us to investigate whether *M. bagoti* foragers learned to use our experimentally provided landmark and/or whether they learned to use a context-specific local vector based on celestial compass cues to navigate out of the arena. Additionally, if *M. bagoti* learned both a context-specific local vector and the beacon, our rotation tests would allow us to determine how they would respond when these cues are placed in conflict. Specifically, we tested whether the ants would integrate these two sources of information.

## Experiment 1

### Method

### Subjects

Experiment 1 was undertaken with 120 solitary foraging desert ants (*Melophorus bagoti*) from a single nest within

their natural semi-arid habitat at a field site approximately 10 km south of Alice Springs, Northern Territory, Australia, in January–March 2009.

### Materials and apparatus

A circular training arena (diameter = 1.5 m, height = 50 cm) made out of 1-mm-thick sheet metal (inside colour: dark blue; outside colour: light grey) was placed in the field so that the centre of the arena was 5.2 m East of the main nest entrance. A white plastic feeder (~15 cm ( $L$ )  $\times$  ~15 cm ( $W$ )  $\times$  9.5 cm ( $H$ )) was buried in the ground up to its lip in the centre of the arena. Sticks were placed in the feeder so that subjects could easily climb in and out. The arena contained a small opening for subjects to enter and exit (~10 cm ( $W$ )  $\times$  ~4 cm ( $H$ )). The entrance/exit was a small depression in the ground which led under the arena wall. The location of the entrance/exit in the arena was aligned with the nest as shown in Fig. 1a.

A landmark was attached to the interior of the arena indicating the exit location. The landmark was a large yellow diamond constructed of foam-paper (30 cm ( $L$ )  $\times$  30 cm ( $W$ )), positioned directly above the centre of the exit (see Fig. 2a).

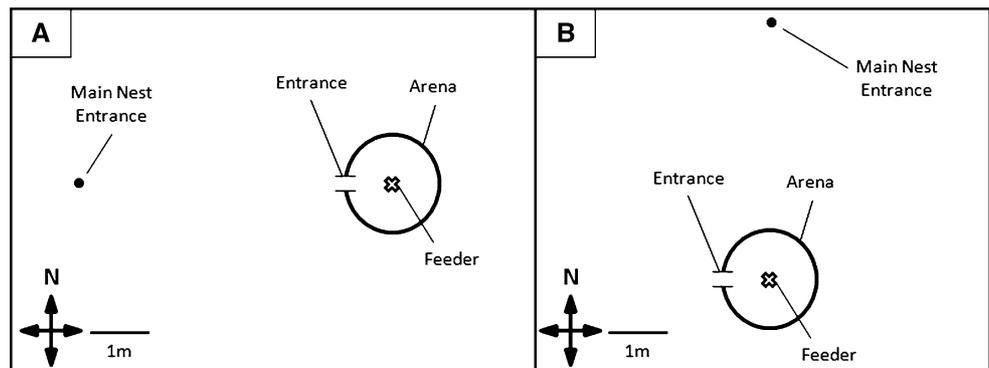
For testing, a second identical arena was placed approximately 7.7 m due East of the nest, measured from the centre of the arena to the main nest entrance. The testing arena did not contain an exit or feeder, but contained a landmark that

was identical to that used in the training arena. Additionally, a large wooden goniometer (60 cm ( $L$ )  $\times$  60 cm ( $W$ )  $\times$  1 cm ( $D$ )) was always present in the centre of test arena. The goniometer contained a small yellow plastic lid (diameter = 3 cm, height = 1 cm) in its centre to provide a starting position for subjects when they were released into the arena. The goniometer was divided into 24 equal sections of 15° each. These sections were numbered from 1 to 24 to simplify the recording of subject headings. Circles were marked at distances of 15 and 30 cm from the centre of the goniometer, allowing us to record a heading at each of these distances. In addition, the 24 directional segments were marked on the arena walls, allowing us to take one final heading when subjects touched the arena wall. The 0° point of the goniometer always pointed in the direction of the nest entrance.

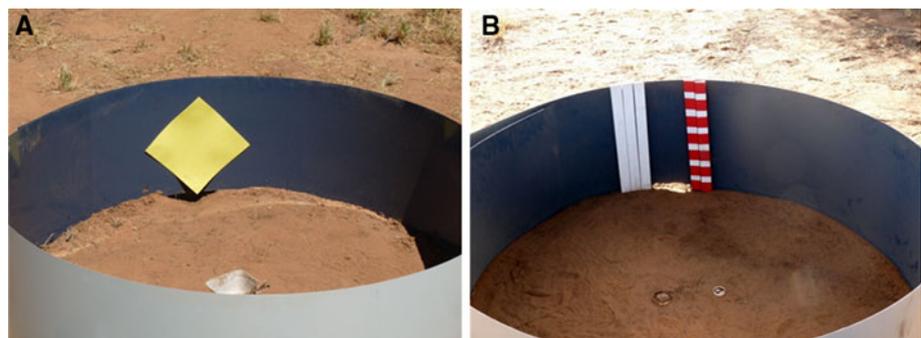
### Procedure

An ample supply of cookie crumbs and/or meal worm pieces were placed inside the feeder and, during training, foraging ants were free to arrive and depart from the feeder. Occasionally, we placed a trail of cookie crumbs leading from the nest to the feeder to encourage new foragers to search for the feeder. On their first observed visit, we captured ants as they left the feeder and marked them with a small dab of acrylic paint on the top of their abdomen. We held the ants while the paint dried and then released them

**Fig. 1** **a** Drawing showing the main nest entrance relative to the arena in Experiment 1. **b** Drawing showing the main nest entrance relative to the arena in Experiment 2. Drawings are to scale



**Fig. 2** **a** Photograph of the arena and landmark used in Experiment 1. **b** Photograph of the arena and landmarks used in Experiment 2



back into the arena to find their way back to their nest. After being painted, ants were left alone to forage and train themselves for at least 1 day before testing. We used different colours of paint for ants on each day, to identify on which day the ant first arrived at the feeder. All ants had a minimum of 1 day of training and at least one visit to the arena on the test day prior to testing, but our observations of the ants' foraging activity indicated that most painted foragers made multiple trips between the feeder and the nest prior to testing. All testing were conducted in the afternoon, between 13:00 and 17:00 hour local time.

For testing, an ant was allowed to enter the training arena and take a piece of food from the feeder. Once the ant exited the feeder, we followed it as it returned to the nest. To prevent the ant from entering the nest, the entrance was temporarily sealed with a glass jar. We observed the ant until it began to take circular paths around the nest area, which indicated that the ant had entered a search mode (Wehner and Srinivasan 1981). Previous research has shown that *M. bagoti* no longer retain a homeward vector once they start their search mode, and hence they are considered to be zero-vector ants (Graham and Cheng 2009a; Narendra 2007b). We then captured the ant near the nest entrance by trapping it within a yellow plastic hoop and scooping it into a small plastic vial. Once caught, we transported the ants in the vial to the testing arena. During transport, the experimenter kept one hand around the vial and another on top to block light and celestial cues.

Once at the testing arena, the experimenter checked to ensure that the ant still held the piece of food. If the ant had lost its food, the experimenter provided it with another piece and watched until it grabbed and held it with its mandibles. The ant was then released from the transport vial into the small lid located at the centre of the goniometer in the centre of the arena. The experimenter stood outside the arena and released the ant by tipping the vial to the side. The experimenter's position relative to the arena was varied across trials. Once the ant was released into the testing arena, we recorded its heading vector when it stepped over the 15- and 30-cm lines on the goniometer, as well as when it first touched the wall of the arena. Once ants had completed a test, they were re-marked with a special colour of paint to denote that they had been tested and to prevent them from being tested more than once.

Four landmark-position tests were conducted, with the landmark placed in the arena at 0, 90, 180 or 270 degrees of rotation relative to the direction of the nest. Both the nest direction and the exit location in the training arena were at 0°.

#### Data analysis

Because the data we collected were directional bearings, we used circular statistics and associated tests (see

Batschelet 1981; Jammalamadaka and SenGupta 2001; Mardia 1972; Upton and Fingleton 1985; Zar 2009). We conducted *V*-tests to determine whether ants were significantly oriented towards the landmark or towards the trained exit direction. The *V*-test determines whether observed angles (i.e., heading directions of each ant) are clustered around an expected angle (Batschelet 1981). In our case, the expected angle is either the location of the landmark or the compass direction at which the exit was located in training. *V*-tests were corrected for the grouping of data into the 15° segments recorded with our goniometer. We also pooled the data in two ways in order to determine whether there was a significant overall orientation towards the landmark or the trained exit direction. To pool the data for landmark orientation, the data were rotated so that the landmark direction always pointed to 0°. When data were pooled to test for orientation towards the trained exit direction, no transformation was applied.

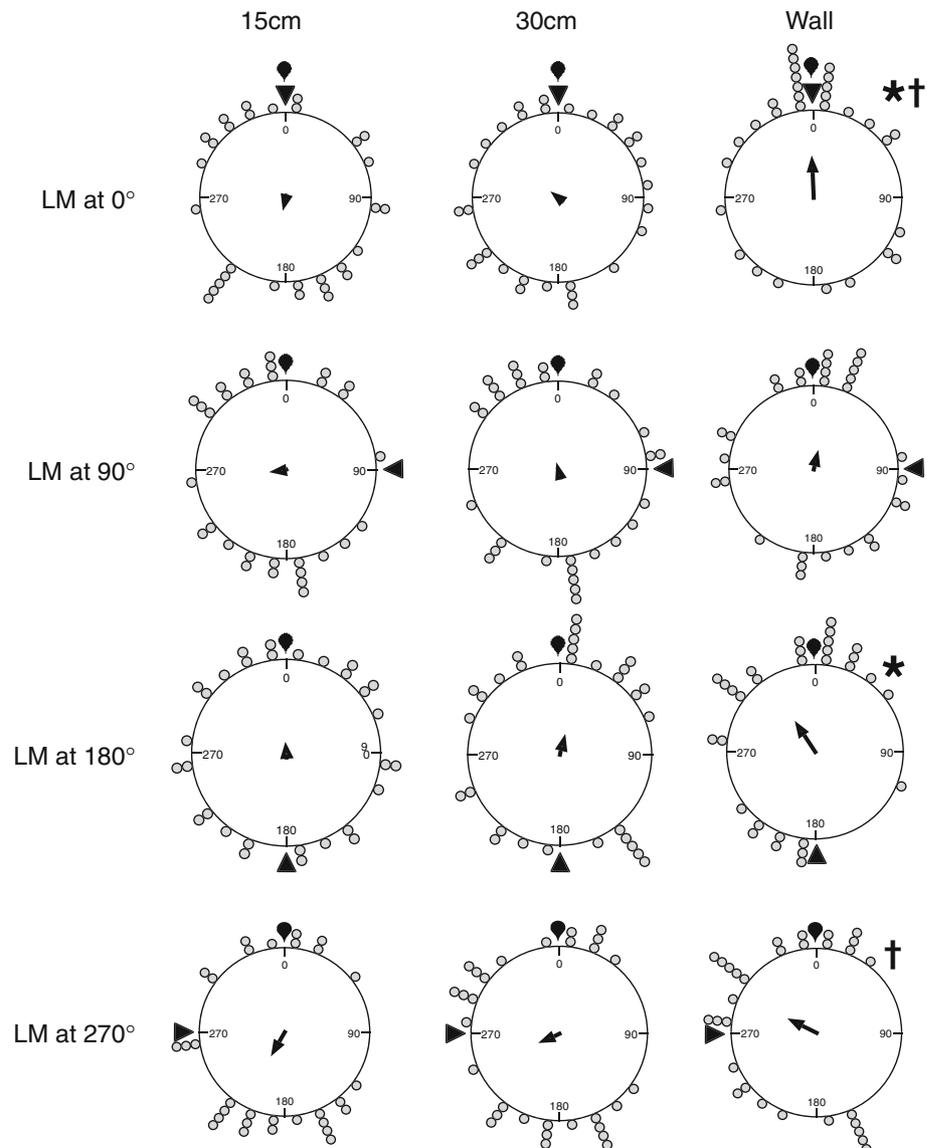
#### Results

Figure 3 shows the results of tests at each of the four landmark rotations. The ants showed clear orientation at the wall when the landmark location was at 0° (i.e., consistent with both the home and trained exit directions). On the other hand, orientation was variable when the landmark was rotated: in some cases (e.g. 270°), ants appeared to be oriented towards the landmark, while in others (e.g. 180°) they appeared to be oriented towards the trained exit direction. Figure 4 shows the data pooled across all tests, ignoring landmark locations (top panels) and pooled across all tests transformed so that the landmark direction always pointed to 0° (bottom panels). This figure shows that over all tests, ants appeared to be oriented more strongly towards the trained exit direction than towards the landmark, at least by the time they reached the wall.

*V*-tests were conducted to determine whether ants were oriented towards the landmark or towards the trained exit direction at distances of 15, 30 and 75 cm (at the wall) for each test condition and for the pooled data. None of these tests were significant after 15 or 30 cm from the centre of the arena ( $P > 0.05$ ). At the wall, orientation towards the landmark was significant when the landmark was at 0° ( $P < 0.001$ ) and at 270° ( $P < 0.05$ ), but not at the other rotations ( $P > 0.05$ ). Orientation towards the exit direction was significant at 0° ( $P < 0.001$ ) and 180° ( $P < 0.01$ ), but not at the other rotations ( $P > 0.05$ ). When the data were pooled, orientation towards the landmark was not significant ( $P > 0.05$ ), but orientation towards the trained exit direction was significant ( $P < 0.001$ ).

To determine whether the ants were integrating a vector between the landmark direction and the trained exit direction when trying to exit the arena, we pooled our data for

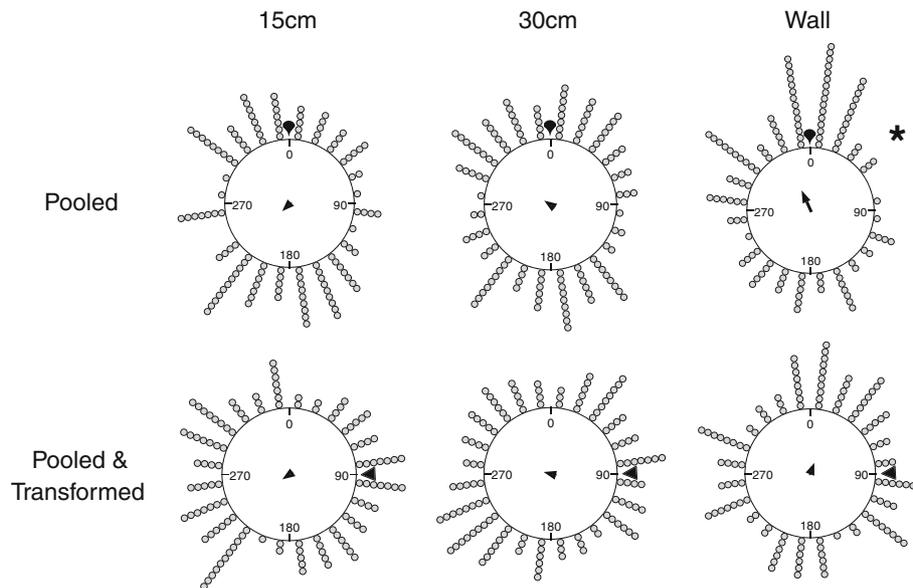
**Fig. 3** Directional bearings of ants at 15, 30 cm and the wall (75 cm) during testing in Experiment 1. The *top graphs* show the test condition in which the landmark was consistent with the trained exit direction and the remaining graphs show the tests in which the landmark was rotated away from the trained exit direction. Each *grey circle* indicates one subject. The *black arrow* extending from the centre of the *circle* indicates the mean vector for the given distribution ( $r$ ). The four values on the outside of the *solid circle* ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ , and  $270^\circ$ ) indicate the angle of deviation from the nest direction. The *dark triangle* indicates where the landmark was located while the *dark teardrop* indicates the trained exit direction. A *asterisk* in the *upper left* corner of a graph indicates that ants were significantly oriented towards the trained exit direction ( $0^\circ$ ) ( $P < 0.05$ ), while a *dagger* indicates that ants were significantly oriented towards the landmark ( $P < 0.05$ ). The nest and trained exit direction was at  $0^\circ$  in all tests. Each graph contains the data from 30 subjects.  $P$ -values reported in this figure caption stem from  $V$ -tests reported in the main text



$90^\circ$  and  $270^\circ$  by reflecting the data collected when the landmark was at  $270^\circ$  along the vertical axis. Ants were assumed to be integrating a vector based on both the landmark and trained exit directions if  $V$ -tests were significant at both orientations (e.g.  $0^\circ$  and  $90^\circ$ ). At 15 and 30 cm,  $V$ -tests revealed that ants were not significantly oriented towards the trained exit direction ( $0^\circ$ ; 15 cm:  $v = -0.119$ ,  $P > 0.05$ ; 30 cm:  $v = -0.035$ ,  $P > 0.05$ ) or the landmark ( $90^\circ$ ; 15 cm:  $v = 0.002$ ,  $P > 0.05$ ; 30 cm:  $v = 0.088$ ;  $P > 0.05$ ). However, at the wall  $V$ -tests revealed that the ants were significantly oriented towards both the trained exit direction ( $0^\circ$ ;  $v = 0.155$ ,  $P < 0.05$ ) and the landmark ( $90^\circ$ ;  $v = 0.158$ ,  $P < 0.05$ ). We then conducted a final  $V$ -test at the arithmetic average between the two points ( $45^\circ$ ) to determine whether the ants were integrating a vector between both the landmark and trained exit directions. This  $V$ -test was statistically significant ( $45^\circ$ ;  $v = 0.221$ ,  $P < 0.05$ )

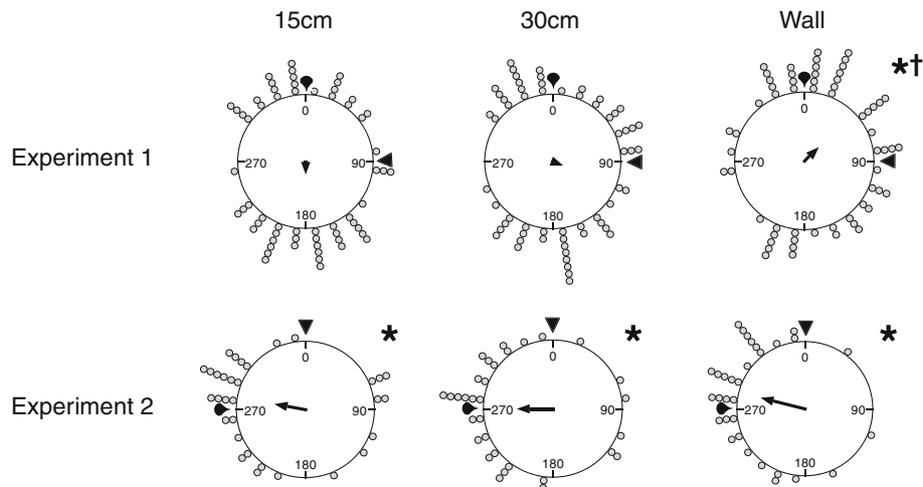
and suggests that the ants were integrating a vector between the landmark and trained exit direction (see Fig. 5, top panel).

Although the ants did not show significant orientation towards either the landmark or the exit direction at 15 or 30 cm distances, an examination of the data suggests that their orientation was bidirectional, with a tendency to head in the exit direction and in its polar opposite. Given that directional ambiguity is consistent with sky compass use, we conducted further statistical analyses to test whether this bidirectional tendency was significant. For these tests, we followed procedures advocated by Batschelet (1981, pp. 21–30, 51). First, we doubled the angles in order to transform the bimodal sample into a unimodal sample (Batschelet 1981, p. 51). We then conducted a  $V$ -test with the expected direction of  $0^\circ$ . Because we doubled the angles, these  $V$ -tests were corrected for the grouping of data



**Fig. 4** Directional bearings of ants at 15, 30 cm and the wall (75 cm) pooled across the four types of tests in Experiment 1 For the top graphs, the data are pooled without transformation. The bottom graphs show bearings in terms of landmark location; for these graphs, the data from landmark rotation tests were transformed by rotating them to place the landmark at 90°. Symbols and other graphical conventions are the same as those described in the caption of Fig. 3. A asterisk in the

upper left corner of a graph indicates that ants were significantly oriented towards the trained exit direction (0°; top panel only) ( $P < 0.05$ ). The nest direction is located at 0° in the top panel. Nest and exit direction cannot be identified in the bottom panel due to the transformation that was applied. Each graph contains the data from 120 subjects.  $P$ -values reported in this figure caption stem from  $V$ -tests reported in the main text



**Fig. 5** Directional bearings of ants at 15, 30 cm and the wall (75 cm) pooled across two landmark locations in Experiment 1 (top panel) and Experiment 2 (bottom panel). In Experiment 1, data were pooled from 90° to 270°. This was done by reflecting the data from the 270° condition across the vertical axis. Thus, all data are pooled at 90°. In Experiment 2, data were pooled from 0° to 180°. This was done by reflecting the data from 180° across the horizontal axis. Thus, all data are pooled at 0°. Symbols and other graphical conventions are the same as those described in the caption of Fig. 3. A asterisk in the upper left corner of

a graph indicates that ants were significantly oriented towards the trained exit direction (0°, top panel; 270°, bottom panel;  $P < 0.05$ ), while a dagger indicates that ants were significantly oriented towards the landmark (90°, top panel,  $P < 0.05$ ). The nest direction is located at 0° in the top panel. The nest direction cannot be determined in the bottom panel due to the transformation that was applied. Each graph in the top panel contains data from 60 subjects. Each graph in the bottom panel contains data from 32 subjects.  $P$ -values reported in this figure caption stem from  $V$ -tests reported in the main text

into the 30° rather than 15° segments. These analyses confirmed that the ants showed significant bidirectional orientation at both 15 cm ( $v = 0.254$ ,  $P < 0.001$ ) and 30 cm ( $v = 0.332$ ,  $P < 0.001$ ).

## Discussion

In this experiment, we found only weak evidence for orientation towards the landmark. However, the pooled results

revealed a strong tendency for orientation towards the trained exit direction at the wall. The initial orientation of the ants at 15 and 30 cm from the centre of the arena was bidirectional and oriented towards the trained exit direction as well as to the polar opposite direction.

The lack of strong orientation towards the landmark is interesting because the landmark was selected to provide a high contrast against the dark wall and was located directly above the exit in training. Based on what is known about vision in *M. bagoti*, we expected that this landmark would provide a salient cue (unpublished data). Moreover, this lack of orientation towards the landmark was surprising because past research has shown that ants (including *M. bagoti*) use artificial landmarks placed at the nest (Narendra et al. 2007) or along a homebound route (Narendra 2007b) as beacons or “signposts” (Cheng 2006). There are several differences between our experimental design and prior studies with *M. bagoti* showing landmark use. For example, our arena blocked all natural panoramic cues. Moreover, our landmark was effectively two dimensional, whereas previous studies used three-dimensional objects as landmarks.

While the ants did not show a strong tendency to orient towards the landmark, and instead seemed to orient more towards the trained exit direction, we pooled our data for 90° and 270° (by reflecting the data collected when the landmark was at 270° along the vertical axis) to determine whether the landmark would show any effect of influencing the directional headings of the ants by causing them to integrate a vector between the trained exit direction and the direction indicated by the landmark. Our analysis revealed evidence that the ants were integrating a vector by the time they reached the arena wall, but did not do so at 15 or 30 cm. While this is the first evidence that *M. bagoti* foragers integrate compass and landmark information, the findings were not exceptionally strong. The topic of the integration of compass cues will require future experimentation to understand in what situations, and to what extent the ants integrate multiple sources of visual information, research that we are currently carrying out.

The significant orientation at the trained exit direction suggests that ants are using some form of compass for orientation (e.g. magnetic, celestial, spectral, etc.). Although the ants were not significantly oriented towards the exit direction at 15 and 30 cm from the centre of the arena, they showed a significant bidirectional orientation towards the exit direction and its polar opposite. The bimodal distribution is a signature pattern for the use of a celestial compass based on the pattern of polarised light (Wehner 1994; see his Fig. 11). The pattern of polarised light, especially in the zenith portion of the sky (which is in fact what the ants saw given the restriction imposed by the test arena), contains a bipolar or 180° ambiguity in indicating the direction of the

sun. Thus, the direction of the sun and its opposite cannot be distinguished by the polarisation compass alone. The ambiguity in the orienting behaviour, however, is still curious because in principle, the pattern of spectral information can be used to solve the ambiguity (Wehner 1994). For example, one side of the wall was brighter than the opposite side. Furthermore, some such source of information must have been used at the wall because the bimodal pattern was replaced by a unimodal pattern of orientation at the wall. Our results therefore point to the possibility that the ants may have learned a context-specific local vector, similar to that described by Collett et al. (1998) to orient towards the arena exit. However, in this experiment, the learned exit direction is also the homeward direction and therefore we cannot rule out the possibility that the ants used a global vector provided by residual traces of path integration. Although many previous studies have shown that the capture procedures we used completely eliminates path integration information (e.g. Graham and Cheng 2009a; Narendra 2007b), we conducted a second experiment to ensure that path integration could not account for the orientation towards the exit.

## Experiment 2

Experiment 2 was conducted using a new nest of ants and was designed to replicate and clarify the results of Experiment 1. In an attempt to increase landmark salience, we replaced the flat two-dimensional landmark from Experiment 1 with a set of three-dimensional landmarks. To clarify whether the ants had learned a local vector that directed them to the arena exit, as opposed to orienting towards their nest direction, we dissociated the direction of the arena exit from the direction of the nest.

### Method

#### Subjects

This experiment was conducted using 64 *M. bagoti* foragers from a different nest in the same field site as Experiment 1.

#### Materials and apparatus

New training and test arenas were constructed. The apparatus was identical to that used in Experiment 1 with the following exceptions. First, the centre of the training arena was located 4.2 m South of the nest. Second, the entrance/exit was a small rectangular hole cut into the base of the arena wall (17 cm (*L*) × 2.5 cm (*H*)) and was rotated by 90° counter-clockwise from the nest direction. Thus, in contrast to Experiment 1, the home direction and training

arena exit direction were dissociated in Experiment 2 (see Fig. 1b). Third, the feeder was a small white plastic lid (diameter =  $\sim 6.3$  cm, height =  $\sim 1$  cm); as in Experiment 1, it was located in the centre of the arena. Fourth, there were two distinct landmarks, one positioned on each side of the exit. These landmarks were constructed from rectangular pieces of wood and they differed from one another in size, colour and pattern. The landmark to the left of the exit was white with no pattern, while the landmark on the right contained thick red stripes made from red duct tape, interspersed with white paint. The landmark on the left was also larger (13.5 cm (*W*)  $\times$  2 cm (*D*)  $\times$  50 cm (*H*)) than the landmark on the right (9 cm (*W*)  $\times$  2 cm (*D*)  $\times$  50 cm (*H*)) (see Fig. 2b). Finally, the testing arena was located approximately 15.1 m due South of the nest entrance.

### Procedure

The training procedure was identical to Experiment 1. The testing procedure was similar to Experiment 1 except that ants were tested in the morning, between 09:00 and 12:00 hour local time. In addition, we changed the manner in which the ant was released into the test arena. In this experiment, string was attached to the base of the transport jar and the experimenter stepped into the arena and placed the jar upside down onto the lid in the centre of the arena. The experimenter then stepped outside the arena and used the string to lift the jar straight up. As in Experiment 1, the position of the experimenter relative to the arena was varied across trials.

### Data analysis

The data were analysed in the same manner as in Experiment 1.

### Results

Figure 6 shows the results of tests at each of the four landmark rotations. The ants showed clear orientation after 15, 30 cm and at the wall when the landmark location was at  $270^\circ$  (i.e., consistent with the trained exit direction). When the landmark was rotated, the ants remained well oriented in every case towards the exit direction. They showed some orientation towards the landmark at the wall only when it was at  $180^\circ$ , but were clearly not oriented towards the landmark on other tests. Figure 7 shows the data pooled across all tests, ignoring landmark locations (top panels) and pooled across all tests transformed so that the landmark direction always pointed to  $90^\circ$  (bottom panels). This figure shows that across all tests, ants were strongly oriented towards the trained exit direction, but not towards the landmark.

*V*-tests were conducted to determine whether ants were oriented towards the landmark or towards the trained exit

direction at distances of 15, 30 and 75 cm (at the wall) for each test condition and for the pooled data. For the landmark orientation, ants showed significant orientation at 15, 30 cm and at the wall when the landmark was consistent with the trained exit direction ( $P \leq 0.05$ ). They were also significantly oriented at the wall when the landmark was at  $180^\circ$  ( $P < 0.05$ ). None of the other tests were significant for landmark orientation ( $P > 0.05$ ). Orientation towards the exit direction was significant at 15, 30 cm and at the wall for all tests ( $P \leq 0.05$ ). When the data were pooled, orientation towards the landmark was not significant at 15, 30 cm or the wall ( $P > 0.05$ ), but orientation towards the trained exit direction was highly significant at all three distances ( $P < 0.001$ ).

To determine whether the ants were integrating a vector between the landmark direction and the trained exit direction when trying to exit the arena, we pooled our data for  $0^\circ$  and  $180^\circ$  (both separated from the trained exit direction by  $90^\circ$ ) by reflecting the data collected when the landmark was at  $180^\circ$  along the horizontal axis. Ants were assumed to be integrating a vector based on both the landmark and trained exit directions if *V*-tests were significant at both orientations (e.g.  $0^\circ$  and  $270^\circ$ ). At 15, 30 cm and the wall, *V*-tests revealed that ants were significantly oriented towards the trained exit direction ( $270^\circ$ ; 15 cm:  $\nu = 0.389$ ,  $P < 0.001$ ; 30 cm:  $\nu = 0.456$ ,  $P < 0.0001$ ; Wall:  $\nu = 0.59$ ,  $P < 0.0001$ ) but not the landmark ( $0^\circ$ ; 15 cm:  $\nu = 0.072$ ,  $P > 0.05$ ; 30 cm:  $\nu = 0.003$ ;  $P > 0.05$ ; Wall:  $\nu = 0.15$ ,  $P > 0.05$ ) (see Fig. 5, bottom panel). Thus, there was no evidence indicating that ants were integrating a vector based on landmark and local vector information.

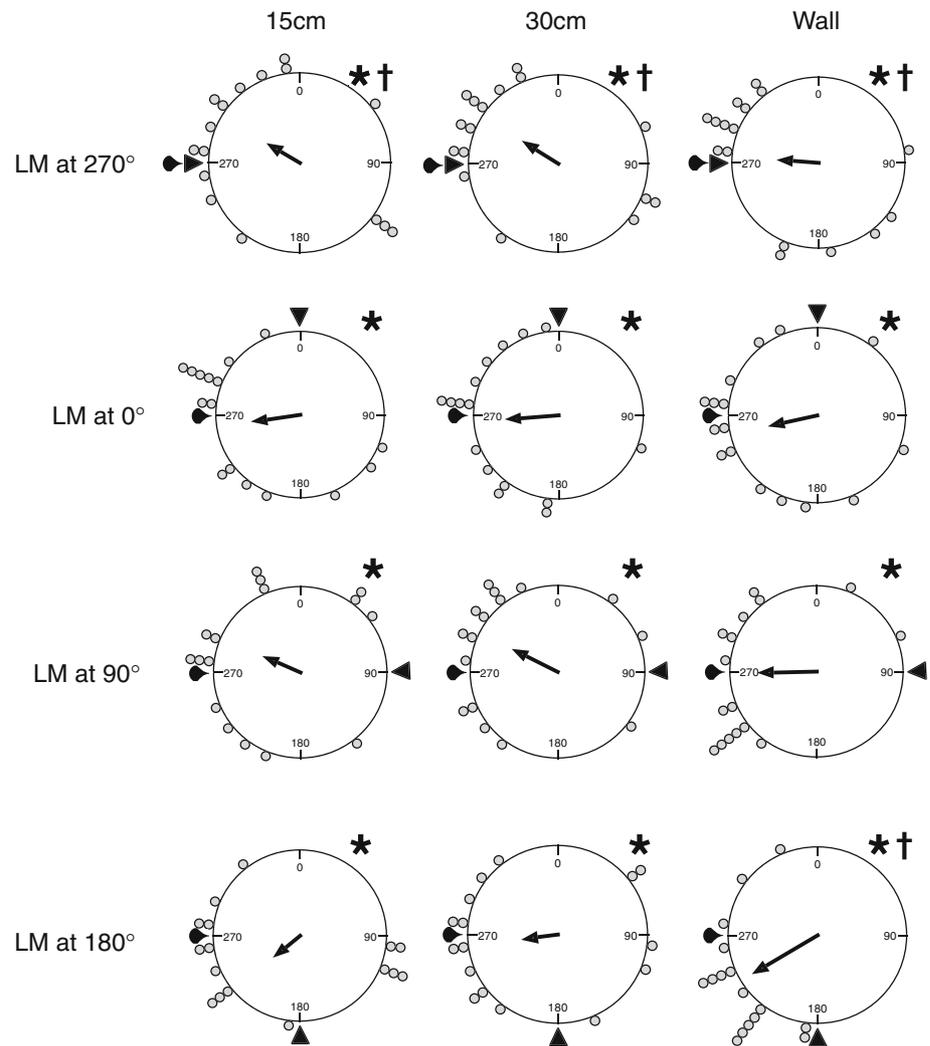
### Discussion

Consistent with results from Experiment 1, the ants showed very strong orientation towards the trained exit direction. Moreover, in this experiment, the ants oriented towards the exit even at 15 and 30 cm from the release point. However, as in Experiment 1, the ants showed little evidence of using the landmarks as beacons to find the exit. Thus, the change to three-dimensional landmarks did not appear to increase the tendency for ants to use the landmarks for orientation.

In this experiment, the significant orientation towards the exit direction was not confounded with homeward orientation because the trained exit direction was rotated by  $90^\circ$  away from the direction to the nest (see Fig. 1). Therefore, the results suggest that the ants learned a context-specific local vector.

While the ants did not show a strong tendency to orient towards the landmark, and instead seemed to orient more towards the trained exit direction, we pooled our data for  $0^\circ$  and  $180^\circ$  (by reflecting the data collected when the landmark was at  $180^\circ$  along the horizontal axis) to determine

**Fig. 6** Directional bearings of ants at 15, 30 cm and the wall (75 cm) during testing in Experiment 2. The *top graphs* show the test condition in which the landmark was consistent with the trained exit direction (270°), and the remaining graphs show the tests in which the landmark was rotated away from the trained exit direction. *Symbols* and other graphical conventions are the same as those described in the caption of Fig. 3. A *asterisk* in the *upper left* corner of a graph indicates that ants were significantly oriented towards the trained exit direction (270°) ( $P < 0.05$ ), while a *dagger* indicates that ants were significantly oriented towards the landmark ( $P < 0.05$ ). The nest and trained exit direction was at 0° in all tests. Each graph contains the data from 16 subjects. *P*-values reported in this figure caption stem from *V*-tests reported in the main text

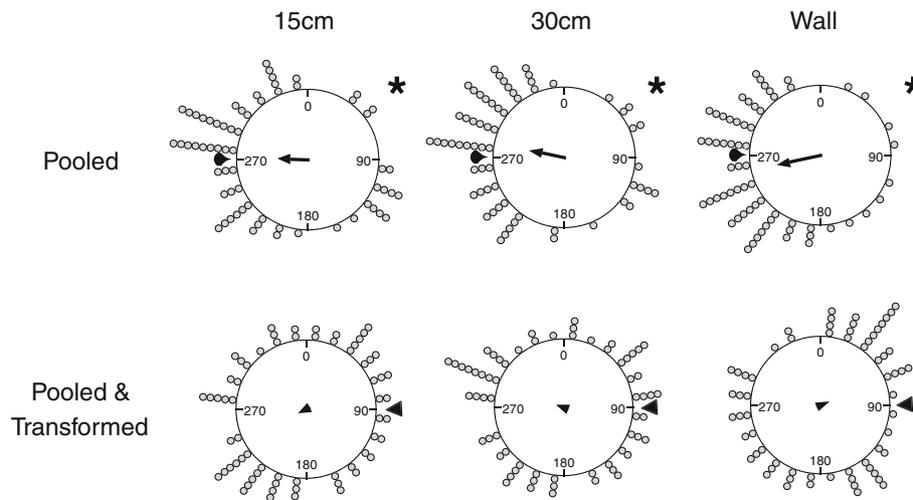


whether the landmark would show any effect of influencing the directional headings of the ants by causing them to integrate a vector between the trained exit direction and the direction indicated by the landmark. Our analysis revealed that the ants did not show any evidence of integrating a vector at 15, 30 cm or at the wall. These findings contradict those found in Experiment 1, thus it is still an open question whether ants integrate vectors based on multiple sources of spatial information.

## General discussion

Our results showed little evidence for landmark use but strong evidence for use of a context-specific local vector specifying a compass direction of travel. Specifically, the ants oriented towards the learned exit direction whether it was consistent with the homeward direction (Experiment 1) or inconsistent with the homeward direction (Experiment 2). This evidence for learning a local vector in *M. bagoti* is

consistent with findings in *Cataglyphis* ants (Collett et al. 1998). Collett et al.'s (1998) *Cataglyphis* ants learned to head south when coming out of an experimentally provided channel and this context-specific local vector appeared to be controlled by compass cues. We suggest that our ants similarly learned a local vector towards the exit direction based on compass information. Presumably, this local vector was activated when the ants were in the context of the arena and motivated to carry food home. The directional instruction appeared to come from compass information gathered from past homebound trips, not from the path integration system calculating progress on the current journey. Path integration was ruled out because we only tested zero-vector ants which no longer have path integration information available (Graham and Cheng 2009a). Moreover, in Experiment 2, the learned local vector was inconsistent with the homeward direction specified by path integration. Experiment 2 also ruled out the use of any remembered global vectors between the feeder and the nest, that is, the vector at the feeder before the ant returned (almost) home and



**Fig. 7** Directional bearings of ants at 15, 30 cm and the wall (75 cm) pooled across the four types of tests in Experiment 2. For the *top graphs*, the data are pooled without transformation. The *bottom graphs* show bearings in terms of landmark location; for these graphs, the data from landmark rotation tests were transformed by rotating them to place the landmark at 90°. *Symbols* and other graphical conventions are the same as those described in the caption of Fig. 3. A *asterisk* in the

*upper left corner* of a graph indicates that ants were significantly oriented towards the trained exit direction (270°; *top panel* only) ( $P < 0.05$ ). The nest direction is located at 0° in the *top panel*. Nest and exit direction cannot be identified in the *bottom panel* due to the transformation that was applied. Each graph contains the data from 64 subjects. *P-values* reported in this figure caption stem from *V-tests* reported in the main text

was captured for a test. This is because the feeder-nest direction was different from the compass direction to the exit of the arena. And it was the latter direction that controlled the ants behaviour. To our knowledge, this is the first evidence that *M. bagoti* foragers can learn a context-specific local vector.

It is not clear which features of the arena were important for defining the context, but we can rule some cues out. Terrestrial cues that appeared above the arena walls were unlikely to play any role. Few cues by way of tall trees were visible above the walls from the centre of the arena. Our test arenas were in any case displaced from the training site, so that any such cues above the walls differed from those found in training. Furthermore, Graham and Cheng (2009a) found that panoramic cues above 27° elevation were neither necessary nor sufficient for zero-vector ants navigating home using panoramic cues. The position of the landmark was also not important as a contextual cue because the ants oriented equally well towards the arena exit no matter where the landmark was. But the arena was a key contextual cue. Once the ants in Experiment 2 had exited the arena, our observations of the ants' behaviour indicated that they no longer headed in the centre-exit direction, but turned to head generally in the nest direction (data not formally recorded).

Surprisingly, our ants showed little evidence of using the experimentally provided landmark information to help them find the exit of the arena. Previous research on *M. bagoti* navigation has indicated that foragers could use landmark information along a route to help them return to their nest

(Kohler and Wehner 2005; Narendra 2007b). To human vision, our landmarks seemed to be the strongest terrestrial cue in the arena because they provided high contrast against the dark walls of the arena. Moreover, they were sufficiently large that they should have been noticeable even with the lower visual acuity of ant vision. Nevertheless, even with the three-dimensional landmarks used in Experiment 2, the ants did not follow the landmarks when they were rotated away from the exit direction. Interestingly, in one case in Experiment 1, after pooling the data from 90° and 270°, we found some evidence for landmark use in the form of it being used as one component of an integration with local vector information. Specifically, at the wall, ants were shown to take an intermediate direction between the landmark and the trained exit direction. While this finding is intriguing, it will need further study to determine under what circumstances *M. bagoti* foragers integrate multiple sources of spatial information. Support for integration was only found at the wall in Experiment 1, and not at 15 or 30 cm, and the finding was not replicated in Experiment 2.

Why did our ants not show strong evidence of landmark use in our experiments? It is possible that while our landmarks were salient to human eyes, they may not have been salient orienting cues to the ants. One possibility, suggested by a reviewer, is that because the two landmarks we used were lighter than the background against which they were placed, the ants may have ignored them. It is possible that ants only use landmarks for orientation and/or navigation when they contrast darkly against the environmental background, as they normally do in nature (e.g. trees

against the sky). However, to our knowledge, there is no research investigating this in solitary foraging desert ants and further testing would be required to determine whether this is indeed the case. Related to this, it is possible that ants only pay attention to landmarks if they are put in contrast with the panoramic skyline. Graham and Cheng (2009b) recently showed that the skyline contour provided by the tops of terrestrial objects, formed a crucial panoramic cue for homebound navigation in *M. bagoti*. The landmarks that we used, being against the walls, did not provide unique skyline information and, as a result, might not have been salient enough to be used for navigation. This was shown to be the case in digger wasps by Tinbergen (1972). Landmarks were most salient to the wasps when they stood up on open ground, cutting into the skyline. Two-dimensional flat landmarks were less salient.

An untested hypothesis worth investigating is that natural objects along a route are salient to the extent that they carve out a chunk of skyline to the navigating ant. Insect vision has limited resolution, and their view-based navigation systems might capitalise on the highest-contrast edges. These are found in the contrast between the tops of terrestrial objects and the sky, the skyline contour. The skyline contains a big jump in overall light level, with the sky being brighter in general than ground objects. But using overall light level to segregate ground from sky requires an adjustable threshold that varies with light level. More promising theoretically is green-ultraviolet (UV) contrast (Möller 2002), with ground objects reflecting more wavelengths that would excite the ‘green receptors’ of insects (Bernard and Wehner 1980; Menzel and Blakers 1976), and the sky providing relatively higher levels of UV wavelengths that would excite the ‘UV receptors’ of insects. Whether insects can and do use such a green-UV opponent-processes channel has yet to be determined.

In conclusion, this paper suggests two novel findings concerning navigation and orientation in the solitary foraging desert ant, *M. bagoti*. First, our experiments showed that *M. bagoti* foragers did not use the experimentally provided beacon landmarks to orient when the global panorama was undifferentiated. In work in progress, we are testing the possibility that landmarks that alter the arena’s artificial skyline will have more influence on the ants’ navigation. Second, our experiments showed that ants can learn a context-specific local vector based on some form of compass. This local vector specifies a compass direction to head to the exit, and is triggered by the context in which *M. bagoti* learns spatial information (being at the centre of the arena with a bit of food to take home). We hypothesise that the compass used to specify the local vector is based on polarised light, as it is in other insects (Wehner 1994), but this remains to be tested. Our findings and the experimental control provided by arenas open up many possibilities for

future research regarding how *M. bagoti* uses different forms of spatial information for navigation.

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**Conflict of interest statement** The authors declare that they have no conflict of interest with the organizations that sponsored this research.

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